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Superparasitism of *Lygus hesperus* Knight Eggs by *Anaphes iole* Girault in the Laboratory[1]

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Anaphes iole **Girault is a solitary egg parasitoid which attacks *Lygus* spp. In a low-parasitoid-density experiment (parasitoid:host ratio = 1:40) 10.0% of available *Lygus hesperus* Knight eggs were superparasitized by *A. iole*. However, in experiments with a high parasitoid density (parasitoid:host ratio = 1:9), superparasitism of *L. hesperus* eggs was 33.3, 66.7, and 82.2% after exposure for 2, 6, and 24 h, respectively. *Anaphes iole* females were likely to superparasitize hosts previously parasitized by conspecific females, as 81.2% of such hosts were accepted for parasitization. High superparasitism rates resulted from a weak tendancy to discriminate against host eggs parasitized by a conspecific and a high rate of encountering such hosts at a high parasitoid density. Female parasitoids demonstrated an ability to discriminate against host eggs that they had recently parasitized, but it was not sufficient to prevent superparasitism from occurring at a high parasitoid density. Mean numbers of ovipositor piercing scars/host egg and parasitoid eggs/host egg increased with, but not in proportion, to the exposure period. The frequency of ovipositor penetrations, without egg deposition, also increased as the exposure period increased at the high parasitoid density. These data suggest that parasitoids are sensitive to some chemical and/or physical changes that occur both on the exterior and interior of the host egg, which causes the host egg to become less acceptable once it has been parasitized. The implications of superparasitization for mass rearing of these parasitoids are discussed.**

Key Words: Anaphes iole; Lygus hesperus; **egg parasitoid; host discrimination; superparasitism; oviposition behavior; insect rearing.**

INTRODUCTION

Superparasitism, the deposition of egg(s) by a parasitoid into or on a host that has already been parasitized with one or more eggs, is commonly reported in field and laboratory studies (Salt, 1961). Parasitoids of many species can discriminate between parasitized and unparasitized hosts and usually avoid ovipositing in the former (Vinson, 1975; van Lenteren, 1976, 1981; van Alphen and Visser, 1990). This discrimination is possible because parasitoids often mark a host that they attack (Roitberg and Mangel, 1988). Some parasitoids can also discriminate between hosts parasitized by themselves or by another conspecific (Hubbard *et al.*, 1987; van Dijken *et al.*, 1992). With solitary parasitoids, a gain in fitness from self-superparasitism is not likely and is a waste of oviposition time and eggs. Conspecific superparasitism can be advantageous under a wider range of conditions, due to the possibility of eliminating a nonsib competitor from the parasitized host (van Alphen and Visser, 1990). Self-/conspecific superparasitism has been studied in few parasitoid species, and that work concentrated on the ability of parasitoids to identify self-parasitized hosts (van Alphen and Nell, 1982; Bai and Mackauer, 1990; van Dijken and Waage, 1987; van Dijken *et al.*, 1992; Gates, 1993; Visser, 1993; Volkl and Machauer, 1990). Superparasitism, however, may be adaptive when the likelihood of finding an unparasitized host is rare (Charnov and Skinner, 1985; van Alphen and Visser, 1990) or when the host egg is already parasitized by a conspecific (van Dijken and Waage, 1987; Hubbard *et al.*, 1987).

The mymarid *Anaphes iole* Girault [= *A. ovijentatus* (Crosby and Leonard)], a solitary egg parasitoid of *Lygus* spp., which is native to western North America (Clancy and Pierce, 1966; Stoner and Surber, 1969; Sillings and Broersma, 1974; Graham *et al.*, 1986; Huber and Rajakulendran, 1988), is a potential candidate for augmentative releases (Debolt, 1987; Jones and Jackson, 1990; King and Powell, 1992). *Anaphes iole*

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parasitizes the eggs of both *Lygus lineolaris* (Palisot de Beauvois) and *L. hesperus* Knight, important North American pests that attack a variety of crops (Graham *et al.*, 1986; Sohati *et al.*, 1989; Rose *et al.*, 1996). Laboratory research on *A. iole* has focused primarily on its biology for mass rearing purposes, using *L. hesperus* as the rearing host (Stoner and Surber, 1969, 1971; Jackson, 1986, 1987; Jones and Jackson, 1990) and some host recognition behavior (Conti *et al.*, 1996, 1997). The ovipositional and host marking behavior and related physical and chemical factors of *A. iole* females parasitizing *L. hesperus* eggs have been described by Conti *et al.* (1996, 1997).

No study of the occurrence of superparasitism in laboratory cultures of *A. iole* has been reported. This study provides information on superparasitism and progeny distribution of *A. iole* over different exposure periods, some behavioral descriptions of parasitoid oviposition and discrimination behaviors when parasitized host eggs are encountered, and discussion of the possible implications of superparasitism for mass rearing.

MATERIAL AND METHODS

Host Rearing and Parasitoid Rearing

Insects used in these experiments were from laboratory cultures maintained at the Biological Control and Mass Rearing Research Unit, Mississippi State, Mississippi. *Lygus hesperus* were reared on an artificial diet (Cohen, 2000), using the basic methods of Patana and Debolt (1985), at 25 ± 1°C, 50–70% RH, and a photoregime of 14:10 (L:D) h. To obtain eggs, a Gelcarin (FMC Corp., Food Ingredients Division, Rockland, ME) oviposition packet (ca. 9 × 9 cm) was placed on the screen top of a cage containing adult *L. hesperus* (Patana, 1982). Females were allowed to oviposit until each packet contained ca. 400–600 *L. hesperus* eggs, which were inserted through the screen and embedded in the Parafilm (American Ca Co., Greenwich, CT) and Gelcarin. Packets with freshly laid eggs were irradiated at 25 Kr (^{137}Cs source) to prevent further embryonic development (Bartlett, 1973; Toba, 1992).

The *A. iole* culture was originally obtained from Biotactics, Inc. (Grand Terrace, CA) and reared on *L. hesperus* eggs. Oviposition packets, containing *L. hesperus* eggs were placed in a 150 × 15 mm plastic petri dish (Fisher Scientific, Cat. No. 08-757-14) and exposed to *A. iole* females for 24 h. After oviposition, exposed packets were placed in a water bath (40°C) to soften the Parafilm and Gelcarin. Parasitized eggs were removed from Parafilm by stretching and agitating it in the water bath and then were placed on filter paper and held in a 100 × 15 mm plastic petri dish (Columbia Diagnostics, Inc., Springfield, VA, Product No. P1015C) containing a water-saturated cotton pad to maintain high relative humidity for 3 days. Eggs were then maintained under the conditions used for *L. hesperus* culture, described above, until adult parasitoid emergence. Adult parasitoids were fed small drops of a 20% honey solution distributed on pieces of Parafilm. Mated adult *A. iole* females (24–48 h old), which had been provided with a 20% honey solution, were used in all of the experiments.

Superparasitism

To quantify *A. iole* superparasitization of *L. hesperus* eggs under a low parasitoid density in the laboratory, the *L. hesperus* eggs, in an oviposition packet containing ca. 400–600 eggs, were counted and the packet was placed in a 150 × 15 mm plastic petri dish. An appropriate number of *A. iole* females, to yield a ratio of 1 female parasitoid to 40 *L. hesperus* eggs, was introduced into the dish (with accompanying males). Adult parasitoids were removed from the dish after 24 h. A similar laboratory experiment was conducted to determine to what extent superparasitism occurred under a high parasitoid density (parasitoid:host ratio of 1:9) with exposure periods of 2, 6, and 24 h. Both experiments were replicated three times. For both experiments, following the removal of the adult parasitoids from the petri dish, the exposed host eggs were removed from the oviposition packet, as described above, and held in a 100 × 15 mm plastic petri dish in an environmental chamber for several hours. Forty-five host eggs per replication and 135 per treatment were randomly selected from the 100 × 15 mm petri dishes and examined using an Olympus SZX12 stereomicroscope (Olympus America, Inc., Melville, NY) to determine if they had been pierced by the ovipositor of an *A. iole* female. Scars left on a host egg after piercing are obvious (Fig. 1). Thirty host eggs, which had been pierced by an *A. iole* female, were then selected and individually dissected, per replication, to determine the number of *A. iole* eggs in each. Host eggs were dissected in a drop of physiological saline on a microscope slide using forceps. The number of parasitoid eggs in each host egg was determined using an inverted stage Olympus IX 70 microscope (Olympus America, Inc., Melville, NY). Using the number of oviposition scars and the numbers of parasitoid eggs found in a host egg, the number of "ineffective ovipositions" (ovipositor pierces without oviposition) or "effective ovipositions" were calculated.

Behavioral Observations

Two experiments were performed to determine if *A. iole* females can identify and discriminate against self- or conspecific-parasitized hosts. The first experiment was conducted in a 150 × 15 mm petri dish containing a packet of ca. 400 host eggs. One inexperienced *A. iole* female was introduced into the arena and allowed to

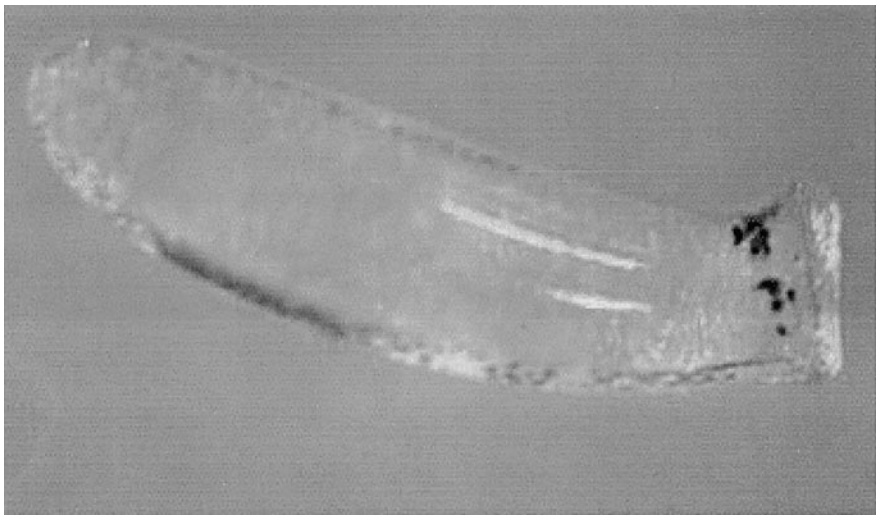

FIG. 1. *Lygus hesperus* egg showing numerous scars near the operculum, indicating ovipositor piercing by *Anaphes iole* females.

oviposit into four host eggs that were close to each other. A small circle was inscribed around the four eggs using a pair of fine point forceps so that the parasitized eggs could be identified. Successful oviposition was indicated if the female marked the host egg after piercing it with her ovipositor (Conti *et al.*, 1997). In the first experiment, after 5 min, the same female was reintroduced into the arena at the location of the four parasitized eggs and allowed to oviposit. In the second experiment, after 5 min, another conspecific female was introduced into the arena at the location of the four parasitized eggs and allowed to oviposit. The behavior of the females was observed continuously using an Olympus SZX12 stereomicroscope. Eggs deposited by *A. iole* females into each of the four monitored host eggs were counted as described above. These experiments were each replicated 12 times.

The final experiment involved introduction of experienced *A. iole* females (1:9 host eggs) into a 150 × 15 mm petri dish containing a packet with ca. 600 fresh *L. hesperus* eggs. Experience was provided by exposing the parasitoids to host eggs for 1 h prior to their introduction into the experimental arena. Four host eggs, which were close together, were selected for monitoring. These four host eggs were monitored, using the stereomicroscope for 30 min. to observe the behavior of females that visited them. After the observation period the eggs were collected and dissected to determine how many parasitoid eggs were in each. This experiment was replicated three times.

Data Analysis

Analysis of variance (ANOVA) was used to detect exposure period effects on percentage of parasitism, superparasitism, parasitoid distribution in the host egg and scar distribution on the host egg. Percentages were transformed by arcsin square root to normalize variance (Sokal and Rohlf, 1981). Means were separated using Student–Newman–Keuls test. Alpha levels were set at 0.05 for all tests. Means are given with ±SEM and those followed by different letters are significantly different at the $P = 0.05$ level. Data analyses were performed with SigmaStat (1994) software.

RESULTS AND DISCUSSION

In the low parasitoid density experiment, the mean percentage of host eggs that had been pierced by *A. iole* females after 24 h was 89.3 ± 2.8%. The percentage of pierced host eggs that contained more than one parasitoid eggs was 10.0 ± 2.7% and the mean number of parasitoid eggs per parasitized host egg was 1.0 ± 0.05. These results indicate that if host eggs are available in sufficient numbers female *A. iole* are able to discriminate between parasitized and unparasitized hosts and will usually avoid ovipositing in the former. These results are consisted with those of Vinson (1975), van Lenteren (1976, 1981), and van Alphen and Visser (1990). Jones and Jackson (1990) reported that an *A. iole* female could oviposit 42.6 eggs in 24 h. Thus, at the low parasitoid density of one parasitoid per 40 *L. hesperus* eggs, the number of eggs available for oviposition approached the ovipositional limit of the female.

In the high-parasitoid-density experiment, of the 135 eggs examined after 2, 6, or 24 h of exposure, the mean percentage of host eggs that had been pierced by an *A. iole* ovipositor was 72.6 ± 0.07, 86.7 ± 0.04, and 96.3 ± 0.02, respectively. The means for the 2- and 24-h exposure periods were significantly different ($F = 7.18$; $df = 2, 132$; $P < 0.05$). These data show high rates of host examination, to the point of ovipositor insertion, under our experimental conditions and that the rate of

TABLE 1

Effect of Exposure Period on the Number of *Anaphes iole* Eggs in Parasitized *Lygus hesperus* Eggs[a]

Exposure period (h)	N/replication[b]	Mean % of host eggs (±SEM) with parasitoid eggs (no. eggs per host)				Mean number (±SEM) of parasitoid eggs per parasitized host egg	Percentage total superparasitism
		1[c]	2[d]	3[e]	≥4[f]		
2	30	66.7 ± 0.03g	25.6 ± 0.03g	7.7 ± 0.01g	0.0 ± 0.00g	1.4 ± 0.05g	33.3 ± 0.03g
6	30	33.3 ± 0.05h	35.6 ± 0.02g	17.8 ± 0.04h	13.3 ± 0.04h	2.2 ± 0.23h	66.7 ± 0.05h
24	30	17.8 ± 0.02i	32.2 ± 0.04g	27.8 ± 0.04h	22.2 ± 0.05h	2.6 ± 0.10h	82.2 ± 0.02i

[a] Means in the same column followed by the same letter are not significantly different at 0.05 level (Student–Newman–Keuls Test).
[b] Total of three replications.
[c] Results for ANOVA (based on a square root, arcsine transformation of proportion): $F = 42.34$; $df = 2, 87$; $P < 0.05$.
[d] Results for ANOVA (based on a square root, arcsine transformation of proportion): $F = 2.68$; $df = 2, 87$; $P < 0.05$.
[e] Results for ANOVA (based on a square root, arcsine transformation of proportion): $F = 6.51$; $df = 2, 87$; $P < 0.05$.
[f] Results for ANOVA (based on a square root, arcsine transformation of proportion): $F = 9.81$; $df = 2, 87$; $P < 0.05$.

such examinations increases with exposure. After 24 h, it would be difficult for a female *A. iole* to find a host egg that had not been previously examined and possibly oviposited in. The mean number of scars per host egg, 1.5 ± 0.14, 2.6 ± 0.49, and 4.1 ± 0.02 for 2, 6, or 24 h of exposure, respectively, also increased with exposure. Again, the means for 2- and 24-h exposure periods were significantly different ($F = 13.56$; $df = 2, 87$; $P < 0.05$). Of the 90 pierced eggs selected for dissection, after 2, 6, or 24 h of exposure, the mean percentage of superparasitized host eggs was 33.3 ± 0.03, 66.7 ± 0.05, and 82.2 ± 0.02, respectively. The data show that, under these experimental conditions, superparasitism was relatively common, compared with the low-parasitoid-density experiment, and increased significantly with the increasing exposure ($F = 42.34$; $df = 2, 87$; $P < 0.05$). The distribution of parasitoid eggs within the parasitized host eggs is given in Table 1. The mean percentage of host eggs containing 1, 2, 3, and ≥4 parasitoid eggs varied with exposure period. The mean percentage of host eggs containing 1 parasitoid egg declined with increased exposure, while the mean percentage of host eggs containing 3 or ≥4 parasitoids was increased (Table 1). As a result, the mean number of parasitoid eggs per parasitized host egg increased with exposure. There is a significant difference in the mean number of parasitoid eggs per parasitized host egg between 2 and 24 h, but not between 6 and 24 h ($F = 35.68$; $df = 2$; 87; $P < 0.05$). We have observed as many as 15 parasitoid eggs in a single host egg. Yet *A. iole* demonstrates an ability to refrain from ovipositing in host eggs that have been parasitized, as the number of parasitoid eggs per parasitized host eggs did not increase significantly from 6 to 24 h of exposure (Table 1). The tendency to avoid oviposition in previously parasitized hosts may be sufficiently strong to effectively eliminate superparasitism under natural conditions, but not under the artificial conditions of the high parasitoid density experiment. Figure 2 shows that the percentage of effective oviposions in eggs with one to seven ovipositor piercing scars. When a female pierced a host egg that had not been parasitized, there was virtually a 100% probability of oviposition (Fig. 2). However, the probability of oviposition decreased to ca. 80% if the host eggs had been pierced and oviposited in one time and then stabilized at ca. 60% for host eggs pierced more than twice. These data indicate that *A. iole* females are able to detect internal chemical or physical differences between parasitized and unparasitized eggs with sensors on their ovipositor (Fisher, 1971), in addition to the external mark reported by Conti *et al.*, 1997.

When a female was reintroduced into an arena in which she had oviposited into host eggs, she often marked those eggs, without any ovipositional behavior (probing or penetrating), after a very short antennal examination and then walked away. Of the 48 host eggs under observation a mean of 81.3 ± 18.0% of the previously parasitized eggs that were contacted were rejected. However, when a conspecific female was introduced into an arena with parasitized hosts, a mean of only 18.8 ± 10.8% of the previously parasitized eggs

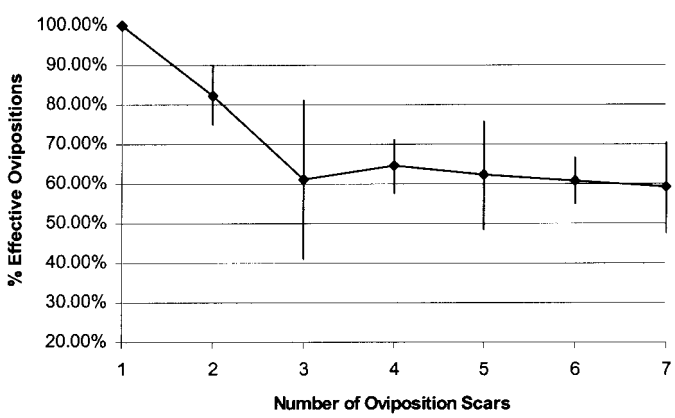

FIG. 2. Percentage of effective ovipositions in *Lygus hesperus* eggs held with *Anaphes iole* for 24 h.

that were contacted were rejected. These results indicate a stronger tendency to reject an egg that was previously parasitized by a female than to reject an egg previously parasitized by a conspecific female. The remarking behavior exhibited when a female reencountered an egg, which she had previously parasitized, is evidence that chemical(s) left on the parasitized egg influence the rejection behavior (Roitberg *et al.*, 1988) and this chemical(s) leads females to mark the egg again, rather then oviposite into it. *Anaphes iole* is a solitary egg parasitoid and, generally, only one parasitoid can develop to the adult stage in a superparasitized host. It is important that the parasitoid have the ability to avoid parasitizing an egg into which she had already deposited an egg because such behavior would be wasteful. However, superparasitism of host eggs previously parasitized by a conspecific may be adaptive when the likelihood of finding an unparasitized host is rare (Charnov *et al.*, 1985; van Alphen and Visser, 1990).

We did observe parasitoids marking host eggs after oviposition. A female would rub the operculum of the egg and the surrounding substrate with the tip of her sheathed ovipositor. She would often turn, reexamine the egg with her antennae, and then mark it again. This behavior was repeated three to six times. Conti *et al.* (1997) reported that when oviposition occurred, an *A. iole* female marked eggs externally and if she reencountered that egg she would antennate it and then reject it, preventing superparasization. It appears that the high rate of encountering parasitized eggs and the willingness to accept hosts parasitized by conspecifics are the main reasons for the high rates of superparasitism observed in our experiments. The probability that a parasitized egg, among the ca. 600 eggs on the packet, will not be encountered by an *A. iole* female, other than the one that oviposited the initial egg, is relatively low.

Inexperienced females of some parasitoid species readily oviposit in parasitized hosts (van Lenteren, 1976). In most of our experiments, however, inexperienced parasitoids were used on the assumption that the parasitoids would become experienced in a short time. In the experiment in which experienced females were introduced into an arena at a parasitoid:host ratio of 1:9 and 12 specific eggs were monitored for 30 min; of the 12 eggs observed, 1 egg was parasitized once, 9 eggs were parasitized twice, 1 egg was parasitized three times, and 1 egg was parasitized four times. Thus, superparasitism was high (91.7%), even during such a short period of observation, indicating that experienced parasitoids readily superparasitized host eggs under these experimental conditions.

Finally, our interests revolve around the development of an artificial diet-based rearing system for *A. iole.* The results of the studies reported here are encouraging in that it may be possible to collect large numbers of eggs in an artificial oviposition substrate. However, superparasitism in high parasitoid density *in vivo* cultures is likely. Thus, in *in vivo* cultures, an effecient exposure system must be devised to maximize overall parasitism while minimizing wasteful superparasitism.

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